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APOGON ROBBYI, A NEW CARDINALFISH (PERCIFORMES: APOGONIDAE) FROM THE CARIBBEAN SEA

Carter R. Gilbert and James C. Tyler

ABSTRACT

Apogon robbyi, a new species of cardinalfish, is described from a total of 33 specimens from Belize, Isla Providencia (east of Nicaragua), and Jamaica. It is morphologically most similar to *Apogon quadrisquamatus,* and is known to occur sympatrically with that species in Belize. *A. robbyi* differs from *A. quadrisquamatus* in having a distinctively striped pigmentation pattern, a large well-defined caudal spot, and in several morphometric features, most notably a proportionally narrower interorbital space and a smaller orbit. *A. robbyi* has been found in a wide variety of habitats, including grass flats, partially open sand bottoms around the bases of finger and globose sponges, tentacles of anemones, inside live conch shells, and around coral reefs and high relief structures such as artificial reefs at depths of from 1 to 30 m.

In 1988, while engaged in an ongoing study on the behavior and ecology of reef fishes at the Smithsonian Institution marine station at Carrie Bow Cay, Belize (on the Belize barrier reef, 18 km off the nearest point on the mainland), the second author and C. Lavett Smith captured an unfamiliar specimen of *Apogon* possessing a striped pigmentation pattern and a large, prominent caudal spot. The fish had sought shelter (along with two small grunts [*Haemulon* sp.]) in a 20-liter plastic bucket containing coral rubble that had been left in a patchy *Thalassia* seagrass bed near a sailfin blenny (*Emblemaria pandionis*) research site at 1 m depth, just off the lagoon-side dock of the Carrie Bow Cay laboratory. Attempts to find additional specimens were unsuccessful (including reexamination of the bucket left at the original site on subsequent days), and none were located in rotenone samples made earlier in the same area, mostly by G. David Johnson and associates.

Although the specimen did not key out to any known western Atlantic species of *Apogon* included in Böhlke and Randall's (1968) taxonomic key, morphological characters agreed closely with those of the sawcheek cardinalfish, *Apogon quadrisquamatus* Longley. However, Longley's (1934) original description of this species, and with one notable exception all subsequent published accounts and figures, indicate a fish having a largely pallid body with a basically yellowish cast (varying from pale orange to red) and yellow fins (Longley and Hildebrand, 1940: 229, fig. 3; Longley and Hildebrand, 1941: 87; Böhlke and Randall, 1968: 181; Böhlke and Chaplin, 1968: 249; Dale, 1977: 25–26). These also agree closely with detailed color notes made in 1971 by the first author on fresh specimens of *A. quadrisquamatus* from Isla Providencia, in the western Caribbean. In marked contrast to the above, Robins and Ray (1986: 152–153, pl. 28) indicated that "most individuals have indistinct, broad dusky stripes on body," and they figured an individual with a dark body, prominent stripes, large caudal spot, and bright yellow fins. The above simultaneously suggested both an undescribed species and a mystery, but further study was necessarily postponed pending the collection of more material of the striped form.

Twenty-one additional specimens of the striped *Apogon* appeared in a large rotenone sample made in the vicinity of Carrie Bow Cay on 17 September 1990. The specific collection site was an artificial reef composed of partially opened metal drums and boilers (up to about 1.5 m greatest dimension) set at about 6.5

m depth in a *Thalassia* sea grass bed. The grass bordered a sparsely vegetated circular sandy bottom about 50 m in diameter, the site of a "shot hole" where explosions associated with geological exploration of the floor during the early 1960's had led to a long-term loss of vegetation. Six species of *Apogon* initially were distinguished among the 213 cardinalfish specimens included in the sample (subsequent study has raised this total to eight), of which those identifiable as *A. quadrisquamatus* were by far the most numerous. Of the 182 individuals initially referable to this species, 161 were essentially pale, with the only discernible body pigmentation a caudal blotch of variable size and intensity, whereas the remaining 21 possessed the same well-developed stripes and large caudal spot found in the specimen collected 2 years earlier. Although caudal-spot variation in the 161 pale specimens was first assumed to be of no particular significance to the problem at hand, subsequent investigation (discussed below) showed it to be of greater importance than originally suspected.

Two additional collections (totalling six specimens) of the "new" striped form were made in the same area in 1994, with these coming from around the bases of finger and globose sponges as well as around the tentacles of anemones. A canvass of museum collections yielded five more individuals, three from Glovers Reef, Belize; one from Isla Providencia; and one from Jamaica. These specimens were found over a depth range of 1 to 30 m, with most being taken at shallower depths.

Although occurrence of both striped and unstriped individuals in the same collection provided compelling evidence that more than one species was involved, the possibility could not be dismissed that the striped condition might represent unusual intensification of a normal but typically latent pigmentation pattern in *Apogon quadrisquamatus*. This condition could be further manifested by increased size and intensity of the caudal spot, which would seem to be in accord with the general perception that this character is typically variable in *A. quadrisquamatus* (compare illustration in Böhlke and Chaplin [1968: 249] with Fig. 2a–b [this paper]). Although variability in this character does exist, the supposed degree of variation may also have resulted partly from confusion with the recently-described *Apogon mosavi,* which had previously been identified as *A. quadrisquamatus* and for which one of the main distinguishing features is a large, dark, rectangular bar situated at the caudal-fin base (Dale, 1977: fig. 1) (Fig. 3a [this paper]). Caution was also dictated by the absence of any noticeable meristic differences between striped and unstriped individuals, a situation in contrast to that involving other members in this species complex (*Apogon aurolineatus* and *Apogon mosavi*), which differ from each other and from *A. quadrisquamatus* by combinations of predorsal scale counts and gill-raker counts on the lower limb of the outer arch. Finally, caution was further indicated by Principal Components Analysis of morphometric characters (based on 27 different measurements of 38 specimens), which showed overlap between the striped and unstriped forms.

Although PCA results were not conclusive, conversion of values to thousandths of standard length produced values sufficiently different that further analysis seemed in order. Values for interorbital distance and orbital diameter appeared especially distinct, and when graphed showed complete separation (interorbital distance) or nearly complete separation (orbital diameter) of the two forms at all sizes above at least 22 mm SL (Figs. 4–5). Subsequent analyses of all morphometric characters, using the Students *t* test, indicated significant (though less striking) differences in several other characters as well (Table 1). These data, together with consistent differences in pigmentation and sympatric occurrence, convinced

Table 1. Measurements of *Apogon robbyi* and *Apogon quadrisquamatus*, expressed in thousandths of mm standard lengths

	Apogon robbyi			*Apogon quadrisquamatus*			
	Range and $\bar{x}$	SD	SE of $\bar{x}$	Range and $\bar{x}$	SD	SE of $\bar{x}$	t value
[†]Number of specimens	16			22			
Range in standard length (expressed in mm)	22.3–35.9 (29.7)			25.5–58.2 (34.8)			
Predorsal length	411–463 (442.6)	11.87	3.06	422–461 (442.1)	10.87	2.37	0.13
Dorsal base	324–369 (348.8)	12.73	3.29	333–380 (359.8)	10.38	2.26	2.84**
Dorsal insertion to upper caudal peduncle	222–254 (237.4)	9.61	2.48	216–253 (235.4)	8.70	1.90	0.66
[a]Least caudal peduncle depth	155–176 (164.1)	6.05	1.56	137–175 (157.9)	8.47	1.85	2.32*
Anal insertion to lower caudal peduncle	216–269 (241.9)	15.75	4.07	206–259 (233.8)	13.09	2.86	1.68
Anal base	124–147 (135.9)	7.56	1.95	123–149 (133.7)	6.69	1.46	0.95
Pelvic origin to anal origin	224–273 (247.1)	15.23	3.93	228–304 (252.5)	20.88	4.56	1.02
Pelvic origin to branchiostegal junction	259–313 (283.4)	25.41	7.05	241–309 (274.4)	15.77	3.44	1.25
Snout to branchiostegal junction	115–173 (138.2)	18.22	5.26	120–199 (156.7)	24.09	5.26	2.56**
Pectoral origin to dorsal origin	227–260 (245.2)	10.14	2.62	231–275 (248.2)	13.75	3.00	0.78
Dorsal origin to pelvic origin	362–405 (377.2)	12.65	3.27	337–395 (369.0)	14.47	3.16	1.88
Dorsal origin to anal origin	405–457 (429.2)	14.16	3.65	397–455 (419.6)	13.71	2.99	2.08*
Dorsal origin to anal origin	440–472 (455.7)	10.96	2.83	424–470 (452.5)	12.58	2.81	0.81
Dorsal insertion to pelvic origin	385–490 (471.5)	25.17	6.50	435–516 (475.1)	16.10	3.51	0.50
Dorsal insertion to anal origin	280–322 (305.1)	10.94	2.82	271–311 (291.8)	10.76	2.35	3.72**
Dorsal insertion to anal insertion	194–217 (205.4)	7.47	2.00	173–222 (198.5)	10.12	2.21	2.37*
Dorsal insertion to lower caudal peduncle	289–332 (307.1)	14.01	3.74	290–324 (304.7)	9.32	2.03	0.57
Anal insertion to upper caudal peduncle	276–318 (300.5)	12.88	3.33	273–308 (289.0)	10.01	2.18	2.99**
Pectoral origin to pelvic origin	135–154 (143.3)	5.05	1.30	130–148 (137.7)	4.48	0.98	3.52**
Pectoral origin to branchiostegal junction	323–368 (339.5)	12.14	3.37	281–368 (326.6)	21.92	4.78	2.25*
Snout to top of gill slit	353–372 (362.2)	5.30	1.37	356–393 (369.4)	9.77	2.13	2.93**
[b]Snout length	85–98 (89.5)	3.28	0.87	75–100 (91.0)	3.75	0.82	2.55**
[c]Orbital diameter	125–139 (134.1)	6.55	1.69	131–168 (148.0)	7.71	1.68	4.26**
[d]Bony interorbital	72–81 (78.0)	2.90	0.75	82–104 (91.6)	5.02	1.10	8.85**
Longest pectoral ray	222–254 (240.5)	9.73	2.81	221–263 (239.9)	11.55	2.58	0.17
Longest pelvic ray	196–241 (221.9)	12.60	3.37	196–245 (228.2)	12.02	2.62	1.54
Depressed dorsal-fin length	236–286 (260.2)	14.25	3.68	216–264 (245.2)	13.50	3.02	3.24**
Depressed anal-fin length	202–246 (229.0)	15.71	4.20	193–256 (227.6)	16.35	3.57	0.26

* Significant difference (95–99 percent confidence level)
** Highly significant difference (99 percent or higher confidence level)
[†] Number of measured specimens and range in standard length of *Apogon quadrisquamatus* as indicated in table, with following exceptions: a. Least caudal peduncle depth—51 specimens b. Snout length—52 specimens c. Orbital diameter—55 specimens; largest measured specimen 45.0 mm SL d. Bony interorbital—55 specimens; largest measured specimen 45.0 mm SL

us that we were dealing with a distinct species, hereafter referred to as *Apogon robbyi*.

The small total sample size (33) of the new species, from only three geographic localities in the northern and western Caribbean, suggests that this fish is neither common nor especially widespread, particularly considering the relatively shallow and accessible habitats from which it has so far been collected. By contrast, *Apogon quadrisquamatus* is known from numerous collections totalling several hundred specimens, occurs over a broad depth range (1 to 65 m), and is distributed throughout much of the tropical western Atlantic region from the southwestern Gulf of Mexico, southern Florida and the Bahamas, throughout the West Indies and Caribbean Sea south to northern Brazil.

Considering its apparent rarity, it is surprising that a specimen of *Apogon robbyi* was the basis for both the color illustration and descriptive account of *Apogon quadrisquamatus* appearing in the Peterson field guide to western Atlantic marine fishes (Robins and Ray 1986: 152–153, pl. 28). The illustration is an artist's rendition of a color photograph taken by Patrick L. Colin of a specimen from Jamaica (UF 229818), and also accounts for that portion of the description in which the species is indicated as having "indistinct, broad, dusky stripes on the body."

Materials and Methods

Complete data were taken on 16 *A. robbyi* and 22 *A. quadrisquamatus* for 14 meristic and 28 morphometric characters, of which one (caudal-fin length) was later eliminated from the analysis since the caudal fin was broken and thus not measurable in a high percentage of individuals. Additional measurements also were made for certain characters that proved to be different or were suspected of being so (e.g., interorbital distance, orbital diameter, snout length, and caudal-peduncle depth). These are indicated at the end of Table 1.

All body-length measurements are in standard length, hereafter indicated as SL. Counts were made based on methods described by Hubbs and Lagler (1958), as were some measurements (standard length, least interorbital distance, orbital diameter, snout length, dorsal-fin origin, caudal-peduncle depth). The fin insertion is considered to be the *posterior* margin of the fin base. This differs from the definition seen in many publications, in which the insertion refers to the *anterior* margin of the paired (i.e., pectoral and pelvic) fin bases. The fin origin, as used in this paper, refers to the farthest anterior margin of the fin base for *all* fins, regardless of whether they are single or paired.

Most measurements were taken (using dial calipers read to the nearest 0.1 mm) as linear distances between landmarks of form (i.e., truss measurements), as illustrated by Schaefer and Cavender (1986: fig. 3). The advantage to using a truss system of measurement is "that bias toward distances along conventional visible axes is avoided and a more even areal coverage in the description of shape change is achieved" (Schaefer and Cavender, 1986: 124).

Body circumferential-scale counts were made in a series between the spinous and soft dorsal fins. Because of irregularities associated with the location of scales on the midline of the belly, however, it was difficult to make accurate counts for this particular series. Counts for the diagonal scale series below the lateral line were made upward and forward beginning at a point just behind the origin of the anal fin, rather than at a point exactly at the origin of the fin. To begin at the latter point would have increased this count by one (seven vs. six), since this would have resulted in inclusion of a tiny scale located just above the origin of the fin. Gill-raker counts include all rudiments. Usually no problem was involved in deciding whether to include the gill raker located closest to the apex of the arch in counts for the upper or lower limb. This sometimes presented a problem, however, and when this structure was situated precisely in the center of the apex it was included with the lower-limb counts.

Although morphometric data were initially taken on specimens of all measurable sizes, these were later restricted to individuals of 22.0 mm SL or greater, because we observed that the accuracy with which certain critical measurements could be made declined significantly at smaller sizes. For example, least interorbital distance normally is a measurement made with considerable accuracy, but in very small apogonid specimens (here defined as those less than 22 mm SL) ossification is notably weaker and it becomes very difficult to distinguish between the supraorbital edge of the frontal and the rim of firm connective tissue immediately laterad. This is particularly important in the present study, since least interorbital distance proves to be of critical significance for distinguishing the two species.

Visual inspection of meristic data revealed no differences between *Apogon robbyi* and *A. quadrisquamatus,* and these data thus were not subjected to further analysis. Morphometric data were logarithmically transformed and principal components were computed from the covariance matrix. Individual measurements were also converted to thousandths of standard length and analyzed using the Students *t* test (Table 1). As indicated earlier, additional measurements were made for several characters found to be, or suspected of being, significantly different and these were included in the analyses. The two measurements showing the highest *t* values (i.e., interorbital distance and orbital diameter) were individually graphed (Figs. 4–5).

In analyzing degree of fusion of the hypural bones from radiographs, difficulty was sometimes encountered in determining when to consider hypural bones 1 and 2 or 3 and 4 fused. Since lines of demarkation between these bones are often visible along all or part of the margins, these bones could be interpreted as lying flush against one another (thus separate) rather than actually being fused. Dale (1977: 25, table 1) considered these bones to be separate only if there was a clearly defined and relatively wide separation over the entire length, as shown by him (Dale, 1977: fig. 2C) for *Apogon maculatus.* Dale's criteria were followed in the present study, and our interpretation of radiographs of the caudal skeleton were confirmed by him (G. Dale, pers. comm.).

Unless otherwise indicated, all specimens examined of *Apogon robbyi* and other *Apogon* species were collected with rotenone. If collected by other means, this is so indicated in the lists of material examined.

In the lists of material examined, number of specimens and ranges in standard lengths appear in parentheses immediately following the catalogue number. Depths at which specimens were collected have been converted from English to metric measurements, rounded off to the nearest half meter.

Characters included in the diagnosis of *Apogon robbyi* are not repeated in the description unless additional clarification is required.

Radiographs were taken at the C. A. Pound human identification laboratory of the Florida Museum of Natural History with a Hewlett-Packard Faxitron series soft x-ray machine, using Kodak X-Omat TL film.

Localities from which specimens of species closely related to *Apogon robbyi* were examined appear in alphabetical order, other than for the types of *Apogon aurolineatus,* for which the type locality is listed first.

Specimens were examined from the following museum collections: Academy of Natural Sciences of Philadelphia (ANSP); American Museum of Natural History (AMNH); Florida Museum of Natural History, University of Florida (UF); Field Museum of Natural History (FMNH); National Museum of Natural History, Smithsonian Institution (USNM); Peabody Museum, Yale University (YPM). Lots formerly in the Rosensteil School of Marine and Atmospheric Sciences, University of Miami (UMML), the collections of which were recently incorporated into those of the Florida Museum of Natural History (UF), have been recatalogued by adding 200000 to the original UMML number (i.e., UMML 29818 converts to UF 229818).

Apogon robbyi new species
Striped cardinalfish
Figure 1

Holotype.—USNM 338013 (35.9; female with well-developed eggs), Belize: edge of shot-hole northwest of Carrie Bow Cay (west of South Water Cay and east of northern end of Twin Cays), 6.5 m, J. C. and D. M. Tyler, G. D. Johnson, C. L. Smith and R. E. Clark, 17 September 1990.

Paratypes.—Belize: USNM 338014 (14, 12.4–32.0; four largest probable males based on gross appearance of gonads; other specimens unsexed), UF 100385 (6, 22.3–30.9; four probable males and one 29.0 mm SL female; smallest specimen unsexed), preceding two lots collected with holotype; UF 100386 (3, 17.9–33.1; two largest specimens ripe females; smallest specimen sex undetermined), USNM 338015 (3, 19.9–21.0; sexes not determined), AMNH 99839 (1, 18.2; sex not determined), FMNH 98241 (3, 27.3–35.5; largest ripe female, other two probable males). *Colombia (Isla Providencia [=Old Providence]):* UF 23552 (1, 23.2; sex not determined). *Jamaica:* UF 229818 (formerly UMML 29818) (1, 20.6; sex not determined).

Diagnosis.—A species of *Apogon* (subgenus *Apogon*) most similar to *Apogon quadrisquamatus,* with which it shares the combination of 3–4 (usually 4) predorsal scales, 12–14 (usually 12–13) gill rakers on lower limb of outer arch, and usually 16 caudal-peduncle circumferential scales. It differs from that species in having (a) seven well-defined lateral stripes running length of body (vs. no stripes); (b) a large and well-defined, medially situated caudal spot clearly visible

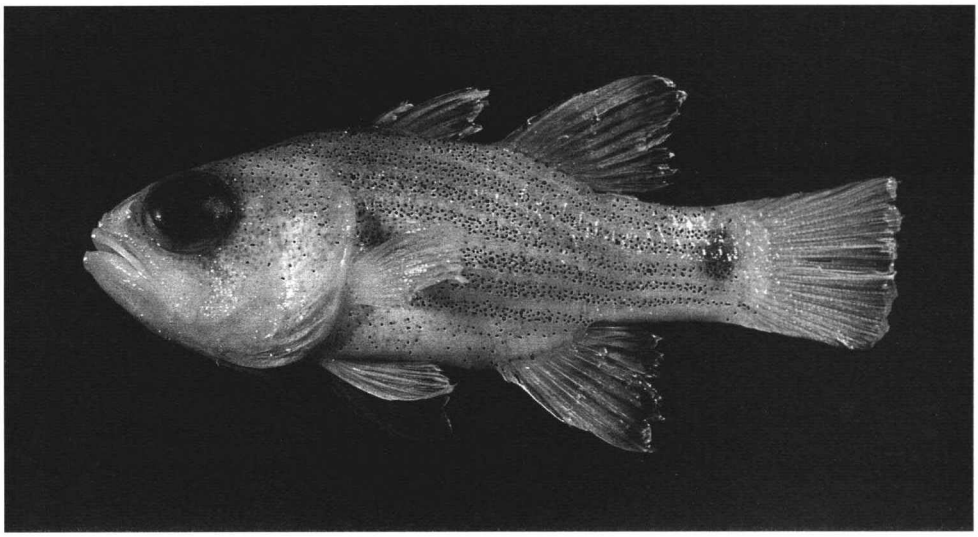

Figure 1. *Apogon robbyi* (holotype), USNM 338013 (35.9 mm SL), Belize: edge of shot-hole northwest of Carrie Bow Cay (west of South Water Cay and east of northern end of Twin Cays), 6.5 m, J. C. Tyler et al., 17 September 1990. (Body striping slightly enhanced).

in well-preserved specimens to as small as at least 18 mm SL, becoming progressively fainter but still visible in smaller specimens including smallest paratype (12.4 mm SL) (vs. a smaller and more weakly defined caudal spot [that in turn may vary from virtually indistinguishable to a fairly prominent caudal bar (Böhlke and Chaplin, 1968: 249; also this paper, Fig. 2a–b)]), (c) highly significant differences for nine morphometric characters (all specimens measured greater than 22 mm SL) (Table 1), the most notable of which are a consistently narrower interorbital space (72–81 vs. 82–104 thousandths SL) (Fig. 4); and (d) usually a smaller orbital diameter (125–139 vs. 131–168 thousandths SL) (Fig. 5) in specimens above 22 mm SL, which affords a separation of at least 75%.

A. robbyi also may reach a smaller maximum size than *A. quadrisquamatus* (largest known specimen of *A. robbyi* slightly less than 36 mm SL). Although additional specimens are necessary to confirm this, small size is suggested by the presence of several gravid females in the type series. By contrast, *A. quadrisquamatus* is occasionally known to reach 58.2 mm SL (the holotype; USNM 107325) and often exceeds 40 mm SL.

Life colors for *A. robbyi* as in Robins and Ray's (1986: pl. 28) illustration of *A. quadrisquamatus,* which is based on only specimen recorded from Jamaica (UF 229818). Body without xanthic pigment in life, but fins lemon yellow with thin red stripe near base of anal fin and red stripe closely bordering base of second dorsal fin. (Based on color slides of live specimens from Carrie Bow Cay [UF 100386, USNM 338015, AMNH 99839]). Adult life colors of *A. quadrisquamatus* with entire body deep rose-red, with darker red bordering bases of second dorsal and anal fins, bright orange-red along first and second dorsal spines, as well as outer half of third dorsal spine and on intervening membranes. (Based on color notes taken in 1971 on fresh specimens from Isla Providencia [UF 23424 and UF 24793]).

Morphometric comparisons appear in Table 1 and the two showing the greatest differences are graphed in Figures 4–5.

Figure 2a. *Apogon quadrisquamatus,* UF 23424 (35.6 mm SL), Colombia (Isla Providencia): east side of island, just north of middle island of "Three Brothers," 3–12 m, C. R. Gilbert and J. Hunt, 24–25 August 1971. (Caudal spot slightly enhanced). Figure 2b. *Apogon quadrisquamatus,* UF 46567 (34.7 mm SL), Bahamas: Little Bahama Bank, north of Memory Rock, D. B. Snyder, 27 June 1983.

Description.—Dorsal rays VI-I, 9 (last ray composite); anal rays II, 8 (last ray composite); pectoral rays 12 (I, II); total gill rakers on outer arch 17–18, those on upper part of outer arch 4–5 and those on lower part of outer arch 13–14 (usually 13); caudal-peduncle circumferential scales 7 + 2 + 7 = 16; body-circumferential scales 5 + 2 + 15 = 22; scales above lateral line 2; scales below lateral line 6; lateral-line scales 24; vertebrae 10 + 14 = 24; serrae along vertical limb of free preopercular margin 11–17; pseudobranchiae 12–14.

First dorsal spine slightly less than 2.0 times in length of second dorsal spine; second dorsal spine about same length as third; spine of second dorsal fin about 1.1 times in second spine of first dorsal fin; pelvic fins extending almost to origin of anal fin; innermost pelvic ray connected to body by membrane at or just beyond halfway out on its mesial branch; pectoral fins reaching posteriorly to base of anal fin; first anal spine about 3.5 times in length of second spine; second anal spine about 1.1–1.2 times in length of spine of second dorsal fin; caudal fin slightly emarginate, the upper and lower lobes rounded.

Upper edge of rear margin of maxilla extending about 5/6 of way back below diameter of orbit; rear margin of maxilla emarginate; upper edge of maxilla slip-

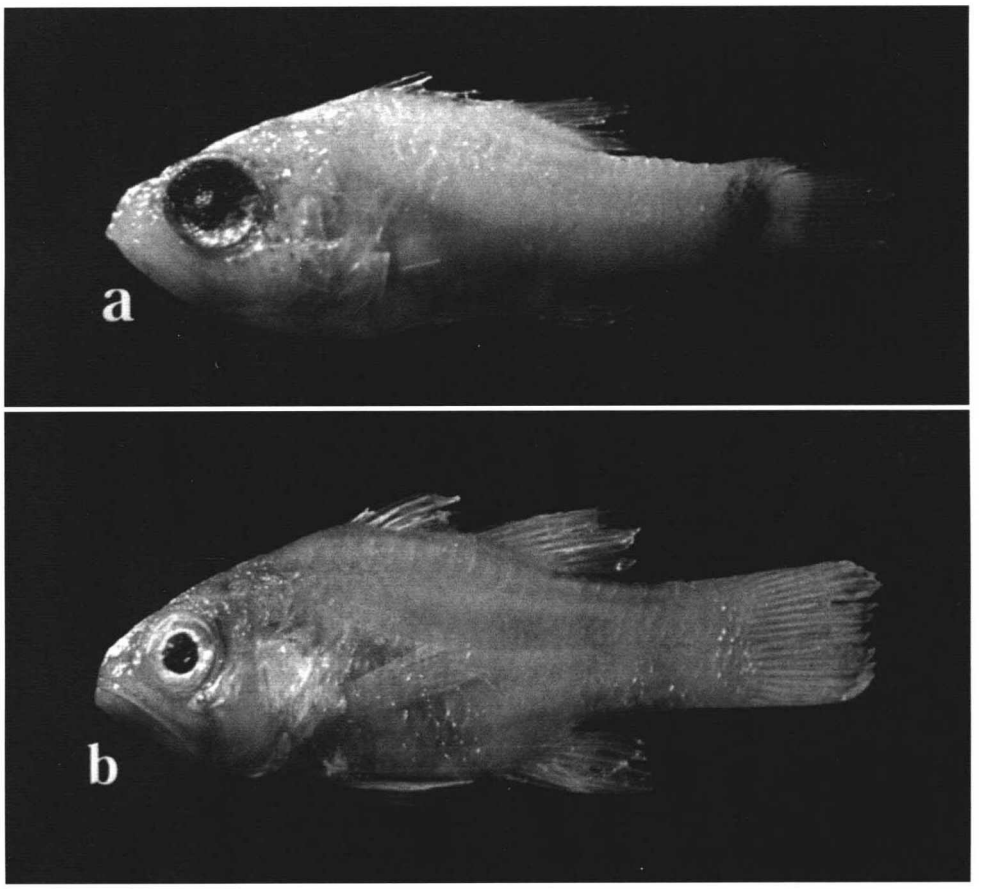

Figure 3a. *Apogon mosavi*, UF 100388 (25.9 mm SL), Belize: edge of shot-hole, northwest of Carrie Bow Cay (west of South Water Cay and east of northern end of Twin Cays) (type locality of *Apogon robbyi*), 6.5 m, J. C. Tyler et al., 17 September 1990. Figure 3b. *Apogon aurolineatus*, UF 10962 (39.0 mm SL), Florida: Florida Keys, quarry on Crawl Key, ca. 9 mi. NE of Marathon, on U.S. hwy. 1, Monroe Co., C. R. Gilbert, C. R. Robins and H. A. Feddern, 23 March 1963.

ping beneath suborbital when mouth is closed; no orbital or anterior preopercular serrations; posterior margin of preopercle finely serrated, the serrations numbering from 11 to 17.

Angle of preopercle formed by a rounded flap of skin that does not extend posteriorly to an imaginary ventral continuation of the line formed by the free posterior preopercular margin; free tip of opercular spine short, pointed and broad based; anterior nostril tubular; posterior nostril a single, near vertical, teardrop-shaped opening nearer eye than to anterior nostril.

Large ctenoid scales present on cheek and opercle; scales on body finely ctenoid, except for those on thorax, nape, and just anterior to pectoral-fin base; lateral line complete; lateral-line scales similar in size to adjacent body scales.

Additional characters common to all members of the subgenus *Apogon* are found in Fraser (1972: 20).

Etymology.—This species is named for Dr. C. Richard ("Robby") Robins, for many years Professor at the Rosenstiel School of Marine and Atmospheric Science

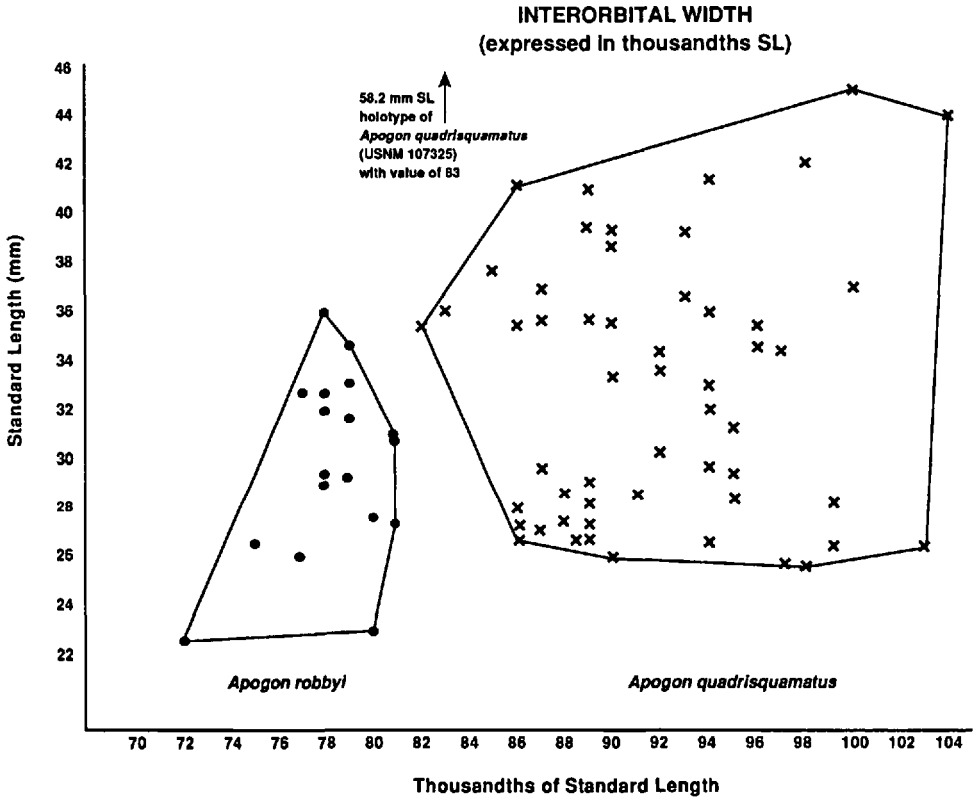

Figure 4. Graphic comparison of interorbital width in *Apogon robbyi* (solid dots) and *Apogon quadrisquamatus* (x's), expressed in thousandths of standard length.

of the University of Miami, and a leading authority on the evolution, taxonomy, and biology of freshwater and marine fishes, particularly those of eastern North America and the western Atlantic region.

Material Examined.—Apogon quadrisquamatus: United States (Florida): USNM 107325 (holotype, probable male, 58.2), Dry Tortugas (presumably vicinity of Loggerhead Key), 20 m, W. H. Longley, no date of collection; USNM 108888 (24 paratypes, 23.3–47.7), same data as lectotype; USNM 213474 (3, 40.7–44.2). *Bahamas:* UF 14315 (3, 410.3-20.8), UF 16645 (1, 24.0), UF 16701 (46, 15.5–36.6), UF 17114 (4, 16.5–28.0), UF 46567 (3, 29.1–34.7). *Belize:* USNM 321021 (6, 17.7–25.4) (same collection as holotype and 20 paratypes of *Apogon robbyi*), FMNH 98113 (5, 13.0–14.3), FMNH 98244 (1, 26.3). *off Brazil:* USNM 213602 (1, 31.2). *Cayman Islands (Grand Cayman):* UF 12339 (1, 23.4), UF 12372 (1, 21.5), UF 14457 (3, 15.0–15.5), UF 14499 (9, 9.0–15.6). *Colombia (Isla Providencia [=Old Providence]):* UF 23424 (11, 17.2–37.8), UF 24793 (10, 26.9–41.2). *off Colombia:* UF 35743 (1, 40.9), USNM 213608 (4, 24.5–38.9). *Cuba:* YPM 462 (1, not measurable) (misidentified paratype of *Amia aurolineatum*). *Curacao:* UF 229782 (formerly 29782) (1, 14.1). *off Honduras:* UF 35742 (1, 45.2). *Jamaica:* UF 228372 (formerly UMML 28372) (15, 12.5–27.4), UF 231181 (formerly UMML 31181) (13, 25.8–29.9), UF 231429 (3, 27.1–36.0). *off Leeward Islands:* UF 35744 (1, 39.3). *off Mexico (Campeche Bank):* UF 30182 (1, 34.5), UF 30275 (2, 30.5–35.6), UF 30293 (2, 41.0–41.6), UF 30375 (1, 39.2). *off Nicaragua:* USNM 179231 (1, 33.9). *Puerto Rico:* USNM 207020 (5, 14.9–22.4). *off Puerto Rico:* USNM 213605 (2, 30.3–33.2), 18°05.5'N, 67°21.5'W, 22 m, trawl, Oregon sta. 5455, 3 June 1965.

Apogon mosavi: Belize: USNM 338016 (155 originally, now 140, 14.4–27.7), UF 100388 (15, 22.1–25.9) (*ex* USNM 338016) (type locality of *Apogon robbyi*). *Bahamas:* UF 13911 (36, 15.8–29.5), UF 14269 (22, 15.5–25.8).

Apogon aurolineatus: Cuba: YPM 461 (34.5) (holotype of *Amia aurolineatum*), Siguanea Bay, Isle

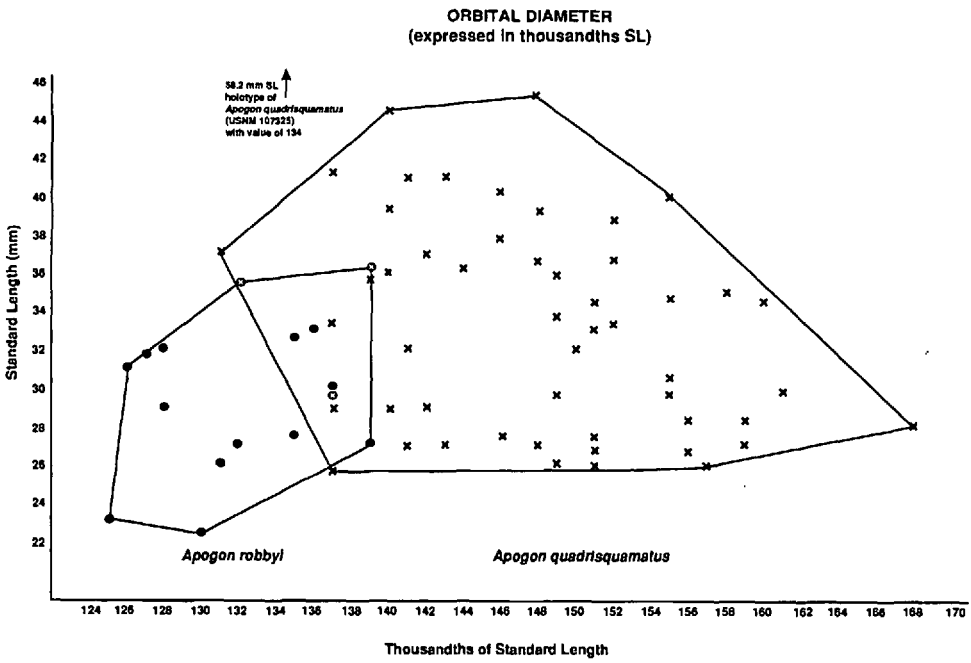

Figure 5. Graphic comparison of orbital diameter in *Apogon robbyi* (solid dots) and *Apogon quadrisquamatus* (x's), expressed in thousandths of standard length. Identical overlapping values indicated by white "x" enclosed within solid dot.

of Pines, Pawnee expedition, 6 April 1925. *Belize:* UF 35741 (1, 26.1), FMNH 98243 (8, 26.0–33.5). *Colombia (Isla Providencia [=Old Providence]):* UF 25593 (1, 16.8), UF 25722 (3, 24.8–34.3). *off Colombia:* UF 100389 (1, 28.6). *Florida:* UF 10962 (5, 32.1–39.0). *off Honduras:* UF 15660 (1, 34.7), UF 100387 (2, 28.7–31.2). *off Nicaragua:* USNM 327991 (1, 29.7). *North Carolina:* UF 77367 (1, 32.8).

Discussion

Comparisons with Apogon mosavi *and* A. aurolineatus.—As indicated above, meristic counts in *A. robbyi* appear identical to those of *A. quadrisquamatus.* These in turn differ from counts for the other two closely related members of the species complex (*A. aurolineatus* and *A. mosavi*) as follows: (a) gill rakers on lower limb of outer arch 12–14 (usually 13) (vs. 14–16 [usually 14–15] in *A. mosavi* and 10–11 in *A. aurolineatus*); (b) predorsal scales 3–4 (usually 4) (overall range in *A. quadrisquamatus* 2 or 5) (vs. 3–4 in *A. mosavi* and 5–6 in *A. aurolineatus*). The caudal-peduncle scale count normally is 16 in all four species, which in turn differs from counts found in most other western Atlantic species of *Apogon.*

The caudal blotch in both *A. robbyi* and *A. quadrisquamatus* usually is more or less circular and confined to the central part of the caudal peduncle (vs. rectangular and nearly reaching upper and lower margins of caudal peduncle in *A. mosavi* [Fig. 3a]; completely absent in *A. aurolineatus* [Fig. 3b]). However, the caudal blotch in *A. robbyi* is consistently large and round (Fig. 1), and appears not to show the variability seen in *A. quadrisquamatus,* in which it may range from small, circular and barely visible (Fig. 2a) to relatively large and rectangular (Böhlke and Chaplin, 1968: 249; also this paper, fig. 2b). The last condition

approaches that typical of the closely related *Apogon mosavi* (see Dale 1977: 21, fig. 1). Further discussion of morphology of the caudal blotch in *A. quadrisquamatus* and *A. robbyi* appears immediately below.

Caudal Blotch.—Published accounts of *Apogon quadrisquamatus* note the presence of a smudgy basicaudal blotch (Böhlke and Chaplin, 1968: 249; Dale, 1977: 26), and Böhlke and Randall (1968: 181), in their taxonomic key to western Atlantic cardinalfishes, listed it as one of the features useful in separating this species from the closely related *Apogon aurolineatus,* in which a blotch is completely lacking. Our observations indicate this character to be more variable in *A. quadrisquamatus* than previously suspected, but note that it still remains an important taxonomic feature. To cite specific examples, three individuals from Little Bahama Bank (Fig. 2b; UF 46567) have a well-developed caudal blotch that in terms of intensity and area is similar to that seen in the specimen of *A. quadrisquamatus* illustrated in Böhlke and Chaplin (1968: 249). (Identification of UF specimens as *A. quadrisquamatus* confirmed by presence of 13 gill rakers on lower limb of outer arch in each individual). Furthermore, the shape of the blotch tends to be more rectangular than usual, and approaches the condition typical of *A. mosavi* (Fig. 3a). In no other specimens of this species available to us did the size, shape and intensity of the caudal blotch equal or come close to the condition in either UF 46567 or the specimen appearing in Böhlke and Chaplin's book. More typically, the blotch appears as a small, discrete mid-caudal spot of varying intensity, as seen in the specimen in Figure 2a (UF 23424) from Isla Providencia. In a series of ten specimens, also from Isla Providencia (UF 24793), seven individuals had a caudal spot similar to that in Figure 2a, whereas in the other three no spot at all was visible to the naked eye. Usually, when no caudal blotch is evident, examination under a binocular microscope shows the tiny melanophores typically scattered over the body of *A. quadrisquamatus* to be more concentrated in the precaudal area (as was the case with the three superficially plain specimens in UF 24793), indicating that a latent caudal blotch is still present.

Caudal-blotch variability was a factor in the original field identification, as *A. quadrisquamatus,* of the entire series of 161 specimens from Carrie Bow Cay, all of which are characterized by pallid bodies and almost all by a large dark caudal bar extending nearly the height of the caudal peduncle (Fig. 3a). We were initially puzzled by the markedly smaller body size of these individuals compared to that of the 21 sympatric specimens of *A. robbyi.* All but two *A. robbyi* exceed in size the largest of the 161 specimens, which was interesting considering that other evidence suggests *A. quadrisquamatus* to be the larger of the two species. We reasoned that this might reflect differences in spawning times (further proof of species distinctness), but did not at first consider the possibility that a species other than *A. quadrisquamatus* might be involved. Closer examination of the 161 specimens indicated, however, that six had a much less distinct caudal blotch than the others. Gill-raker counts on the lower limb of the outer arch of these individuals were 12 or 13 in four and two specimens, respectively, thus confirming their identification as *A. quadrisquamatus* (Böhlke and Randall, 1968: table 1; Dale, 1977: table 2). By contrast, counts on 22 "strongly-blotched" individuals (randomly selected) showed lower-arch gill-raker counts of 14 (13 specimens), 15 (eight specimens), and 16 (one specimen). The combination of higher gill-raker counts and a much enhanced, rectangular caudal blotch confirmed that most specimens in the series (i.e., 155 of 161) were in fact *Apogon mosavi,* a species distinguished by the above two characters as well as a diminutive body size (largest of 816 types, 34.0 mm SL; Dale, 1977). The fact that the six specimens

of *A. quadrisquamatus* in the large Carrie Bow Cay series were all small (range 15.6–24.1 mm SL) is presumably coincidental. The presence of *A. mosavi* at Carrie Bow Cay is of interest, since it not only represents a significant westward range extension of the species (previously recorded from the Bahamas, Haiti, and Jamaica [Dale 1977: 20]), but also confirms the sympatric occurrence of all four members of the *quadrisquamatus* species group at this locality.

Because of its demonstrated variability in *Apogon quadrisquamatus,* we initially considered the large caudal blotch in *Apogon robbyi* to be a less important diagnostic feature than the body stripes. Further analysis, however, showed that the blotch in *A. robbyi* not only remained constant in both size and shape in all specimens examined, but was consistently different from that seen in any of the large number of available specimens of *A. quadrisquamatus.* Although tending to become more obscure in smaller individuals (i.e., below ca. 18 mm SL), it was nevertheless visible even in the smallest (12.4 mm SL) paratype.

Morphometric Comparisons.—Morphometric characters were analyzed using Principal Component Analysis, but only a partial separation of *A. robbyi* and *A. quadrisquamatus* was obtained. When converted to thousandths of standard length and analyzed using the Students *t* test, however, 45 percent of the 27 characters showed differences that were either significant (3) or highly significant (9), which was surprising considering the relatively inconclusive PCA results obtained. As shown in Table 1, those measurements found to be most highly significant were bony interorbital ($t = 8.85$), orbital diameter ($t = 4.90$), dorsal insertion to anal origin ($t = 3.72$), pectoral origin to pelvic origin ($t = 3.52$), and depressed dorsal-fin length ($t = 3.24$).

As can be seen from Figure 4, no overlap in interorbital width was found for any of the 72 total combined specimens of *Apogon robbyi* and *A. quadrisquamatus* (17 and 55 specimens, respectively), with interorbital-width values ranging from 72–81 thousandths SL (mean = 78.0) in *A. robbyi* and from 82–104 thousandths SL (mean = 91.6) in *A. quadrisquamatus.* These differences hold true for all individuals regardless of body size within the size range of specimens measured (i.e., 22 mm SL or larger). A less complete but nevertheless obvious separation (also based on 72 specimens) is also apparent for orbital diameter: 125–139 thousandths SL (mean = 134.1) in *A. robbyi* and 131–168 (mean = 148.0) for *A. quadrisquamatus.* Separation of the two species based on the latter character is estimated to be between 75–80 percent, based on numbers of non-overlapping data points in Figure 5.

Interestingly, the holotype of *A. quadrisquamatus* gave the next to the lowest values for both interorbital distance and orbital diameter (83 and 134, respectively) for any measured specimens of this species (Figs. 4–5). Although these data suggest a possible allometric shift, no such trend was evident among the other measured specimens (22–45 mm SL) (Figs. 4–5), and in fact two of the highest recorded interorbital values were from the next two largest individuals measured (both from USNM 213474) (104 for a 44.2 mm specimen; 100 for a 45 mm specimen) (Fig. 4). Orbital diameter values for the last two specimens were 140 and 147, respectively, both of which are in the middle of the range of values for the species (Fig. 5).

Several other morphometric values obtained for the holotype of *A. quadrisquamatus* were also at or near the extremes found for this species: dorsal insertion to upper margin of caudal peduncle (253), anal insertion to lower caudal-peduncle margin (206), anal base (124), pelvic origin to anal origin (304), dorsal origin to pelvic origin (516), dorsal origin to anal origin (455), caudal-peduncle depth

(175), and dorsal insertion to anal insertion (222). Of these measurements, however, the first five are not among those showing significant differences between the two species, and the last two are not highly significant. We conclude from this that inclusion of the unusually large holotype in the morphometric analysis does not affect the overall results.

Body Size.—*Apogon robbyi* is known to reach at least 35.9 mm SL, in contrast to *A. quadrisquamatus,* which may grow to at least 58.2 mm SL (Longley and Hildebrand 1940). Although the holotype of the latter species is unusually large, individuals greater than 40 mm SL are not uncommon in collections. Since the total number of available specimens of *A. robbyi* is not great (33), the possibility cannot be dismissed that larger individuals of this species may be discovered in the future. However, since some types are mature adults, we think it more likely that *A. robbyi* will prove to be a diminutive species, as is true also for *A. mosavi* (Dale 1977).

Palatine Teeth.—Fraser (1972: 20) listed the presence of palatine teeth as a diagnostic character for the subgenus *Apogon,* and indicated their presence in all members of the group except *Apogon quadrisquamatus.* Our studies show Fraser's observation to be only partly correct. Examination of over 50 specimens indicates the presence of palatine teeth to be variable in this species, ranging from well developed and numerous to completely absent. The former condition is much more common, although surprisingly one of the few individuals lacking teeth is the holotype (USNM 107325), which also is by far the largest known specimen of this species. Equally surprising, all 24 paratypes have the teeth well developed on this bone. In another series of *A. quadrisquamatus* (UF 23424), from Isla Providencia, two specimens had the teeth present but greatly reduced in size and number, whereas in the remaining nine specimens the "normal" condition prevailed. We see no evidence to suggest that the presence or absence of palatine teeth might have a sexual basis, nor does it appear to be a function of size and development. Teeth were evident in all specimens examined under 20 mm SL, and, as noted above, the largest known specimen completely lacks teeth in this region.

Although palatine teeth are present in *Apogon mosavi,* limited observations indicate them to be somewhat less developed than in *A. quadrisquamatus.* Teeth were present in all specimens of *A. robbyi* checked for this character, as they were also in the small number of *A. aurolineatus* examined.

Fusion of Hypural Bones in Caudal Skeleton.—Dale (1977: fig. 2, table 1), in his description of *Apogon mosavi,* discussed and illustrated differences in degree of fusion of the five hypural bones (specifically nos. 1–4) between that species and *A. quadrisquamatus.* The caudal skeleton of *Apogon maculatus* was also illustrated for comparison. He found there to be a significantly greater incidence of fusion involving hypurals 1–2 and 3–4 in *A. mosavi,* with 211 of the 225 specimens analyzed (94 percent) showing fusion of each of these pairs of bones (formula expressed as 1 + 2, 3 + 4, 5). The remaining 14 specimens had a caudal formula of 1 + 2, 3, 4, 5. By contrast, only 71 of the 104 specimens of *A. quadrisquamatus* analyzed (68 percent) had the former combination, with the remainder showing the following: 1 + 2, 3, 4, 5(3); 1, 2, 3 + 4, 5(16); 1, 2, 3, 4, 5(14). (Last condition, which involves no hypural fusions, also typical of *A. maculatus*). Our radiographs of 17 specimens of *A. robbyi* show all the above combinations (i.e., 1 + 2, 3 + 4, 5[7]; 1 + 2, 3, 4, 5[1]; 1, 2, 3 + 4, 5[5]; 1, 2, 3, 4, 5[4]), a situation in agreement with that discussed by Dale for *A. quadri-*

squamatus. Although these observations should be tempered by earlier observations regarding difficulties in interpreting degree of hypural-bone fusion from radiographs, we should also make the observation that the species differences noted by Dale (1977) seem to be confirmed by our readings of additional specimens of *A. mosavi* (27 from two series) and *A. quadrisquamatus* (31 from five series).

Caudal-peduncle Scale Counts.—Although caudal-peduncle scale count has not been accorded any special significance in apogonid classification, it is an important taxonomic character and in some instances may be useful in discerning species-group relationships. Fraser and Lachner (1985: table 1) found it useful for distinguishing certain species of the Indo-Pacific subgenus *Pristiapogon* (genus *Apogon*). The closely related but allopatrically distributed western Atlantic species *Apogon maculatus* and *A. americanus* usually have 20 scales in this series (Gilbert, 1977), and it may be significant that this count is also shared by two other common allopatric species living at a similar depth and habitat, the eastern Atlantic *A. imberbis* and the eastern Pacific *A. dowi* (Fraser and Robins, 1970: table 1). *Apogon leptocaulus* has an unusually low caudal-peduncle scale count of eight that is unique among Atlantic and eastern Pacific *Apogon* species (Gilbert, 1972). (No analysis has been attempted for the Indo-Pacific species). Most of the western Atlantic species of *Apogon* characterized by two posterior bars of varying width and intensity average 12 scales in this series, except for *A. planifrons* in which this count sometimes reaches 16. The three species of *Phaeoptyx (P. pigmentaria, P. conklini, P. xenus)* all have a modal count of 16, as do the four species in the *Apogon quadrisquamatus* species group discussed in this paper. Based on other fundamental differences among *A. planifrons,* the genus *Phaeoptyx,* and the *Apogon quadrisquamatus* species group, the common presence of 16 caudal-peduncle circumferential scales undoubtedly is due to morphological convergence. At the same time, we also regard this derived character as indicating a close interrelationship among the four species here considered to comprise the *A. quadrisquamatus* species group.

Comments on Types of Apogon quadrisquamatus.—Longley (1934) listed a 78 mm total length (=62 mm standard length) specimen as "type" in the original description of *Apogon quadrisquamatus.* Hildebrand (*in* Longley and Hildebrand, 1940: 230–231) pointed out that no individual had been removed or segregated from the type series of 26 specimens, and also that none of these individuals were the same exact length given by Longley for the type. Even though Longley's "type" is over 10 mm longer than the next largest specimen in the type series, Hildebrand hesitated to call it the holotype, since his measurements (75 mm TL; 59 mm SL) were three mm less in each case than those indicated by Longley in the original description. Although Hildebrand acknowledged that the discrepancies in length possibly were due to shrinkage, he nevertheless was uncertain whether the two individuals were the same and accordingly designated the "smaller" specimen (USNM 107325) as lectotype. We feel that Hildebrand was unduly conservative, and have no doubt that his "lectotype" and Longley's "type" are one and the same. The specimen should properly be considered a holotype.

The holotype is remarkable for its unusually large size (58.2 mm SL), which is 10.5 mm longer than the next largest type (as noted above) and 13 mm longer than the next largest individuals seen by us (UF 35742, USNM 213474). This, coupled with the absence of palatine teeth in the holotype, necessitated a close reexamination in order to allay suspicions that the specimen actually might represent a species of *Apogon* different from *A. quadrisquamatus,* as presently con-

ceived. The holotype and all paratypes, although in good condition, are discolored and brown, which makes determination of the original pigmentation pattern difficult. However, microscopic examination reveals numerous tiny melanophores scattered over the body in no discernable pattern, other than being slightly more concentrated in the mid pre-caudal area. Critical meristic characters of the holotype include 13 lower gill rakers (including one barely visible rudimentary raker), four predorsal scales, and 16 caudal-peduncle circumferential scales. Since the above combination of characters agree with those diagnostic of *A. quadrisquamatus,* we conclude that the holotype is properly associated with the sawcheek cardinalfish.

We should note that, although Hildebrand (in Longley and Hildebrand, 1940) indicated a total of 26 specimens (including the "lectotype") in the type series, only 25 are now present. Whether the original count was erroneous or a specimen was subsequently removed is not known.

Relationships.—The presence of horizontal stripes in *Apogon robbyi* is unique among western Atlantic Apogonidae, in contrast to Indo-Pacific members of the family in which striping is found in a number of species belonging to various genera (Lachner, 1953: pls. 35–43). This similarity is only superficial, however. *A. robbyi* clearly is a member of the subgenus *Apogon,* possessing at least 11 of the 14 morphological features listed by Fraser (1972: 20) as characterizing the group (the remaining three characters could not be evaluated from whole-specimen examination or from radiographs). According to Fraser (1972: 18–19), this subgenus includes most Western Hemisphere apogonid species (15 of 17 analyzed by him), with the remaining two species (*Apogon affinis* and *A. evermanni*) each included in its own monotypic subgenus (*Paroncheilus* and *Zapogon,* respectively). By contrast, only four of the total 66 Indo-Pacific species of *Apogon* included in Fraser's classification belong to the nominal subgenus.

Despite strong dissimilarity in pigmentation pattern, *Apogon robbyi* is presumed to have its closest relationships with *A. quadrisquamatus,* based on identical meristic characters. This in turn places it in a species complex that also includes *A. mosavi* and *A. aurolineatus.* Comparison of osteological characters (based entirely on radiographs) has revealed nothing to counterract this assumption.

Ecology

Apogon robbyi has been collected from a wide variety of habitats, most of which are outside the immediate areas of coral reefs. At Carrie Bow Cay, Belize, we have found it in shallow waters in and around *Thalassia* beds and in sparsely vegetated parts of the shot-hole habitats interspersed therein. (Greenfield and Johnson [1990] also recorded *Apogon quadrisquamatus* and *Apogon aurolineatus* from grass habitats around Belize). The largest (i.e., type) series (21 specimens) was observed and collected while the individuals were hovering within the metal containers of an artificial reef at 6.5 m depth in an area bordering a *Thalassia* bed and a shot hole. We have often seen, and sometimes collected, specimens of *A. robbyi* in the more sparsely-vegetated parts of the shot holes themselves (UF 100386), where they were hovering around the bases of finger sponges (the orange sponge, *Raphidophlus juniperinus* [a bush-branched species], and the red finger sponge *Amphimedon compressa* [a single-branched species]), or seeking shelter amongst the tentacles of anemones (*Bartholomea annulata*). It also occurs in *Thalassia* beds per se, as indicated by a collection of three specimens (FMNH 98241) made by David W. Greenfield and Robert K. Johnson at Glovers Reef, and by our first specimen (AMNH 99839), which had settled into a bucket set in

a shallow *Thalassia* bed just off the lagoon-side dock at Carrie Bow Cay. Water depth in both cases was only about, or slightly over, a meter deep.

We have not found specimens of *A. robbyi* among the apogonids included in numerous rotenone collections made in the coral reefs around Carrie Bow Cay. Apparently the only record from this particular habitat is the specimen photographed and collected with quinaldine by Patrick L. Colin in Discovery Bay, Jamaica, at 23–30 m depths (UF 229818), which (as stated elsewhere) is the fish on which the illustration of *A. quadrisquamatus* in Robins and Ray's (1986) field guide was based.

The most unusual record of this species is the specimen (UF 23552) collected within the shell of a large live queen conch (*Strombas gigas*) at Isla Providencia, east of Nicaragua. Also included in this collection were numerous specimens of the conchfish (*Astrapogon stellatus*) and two small lantern bass (*Serranus baldwini*).

It appears from the above that *A. robbyi* utilizes a diversity of habitats for its daylight hovering place. The closest presumed relative for which behavioral information is available, *A. quadrisquamatus,* is known to be nocturnal (Collette and Talbot, 1972) and to feed low in the water column at night over sand flats near coral reefs (Smith and Tyler, 1972). Presumably, *A. robbyi* leaves its daytime hovering places to forage over grass and sand flats at night.

Apogon quadrisquamatus may have even more diverse daylight hovering places than *A. robbyi,* having been reported from small patch reefs and over sand and rubble bottom (Böhlke and Chaplin, 1968); on large coral reef structures (Starck, 1968; Collette and Talbot, 1972); around the bases of *Diadema* sea urchins (Smith and Tyler, 1972); among the tentacles of two different species of sea anemones, *Bartholomea annulata* and *Condylactis gigantea* (Colin and Heiser, 1973, Colin, 1974); within the cavities of a long tubular sponge, *Callyspongia vaginalis* (Tyler and Böhlke, 1972); over open sand bottom (Dale, 1975); and over the open sand and mud bottoms of commercial fishing grounds in the Gulf of Mexico, where it is apparently rare (Bullis and Thompson, 1965, Powell et al., 1972, Williams and Shipp, 1980). Most specimens collected from Isla Providencia came from within the cavities of tubular sponges (species not recorded).

As noted elsewhere, *Apogon robbyi* has been taken sympatrically with its presumed three closest relatives (*A. quadrisquamatus, A. mosavi,* and *A. aurolineatus*) at least once, at the Carrie Bow Cay type locality. *A. robbyi* and *A. quadrisquamatus* also occur at least in the same general area of the grass flats in the lagoon of Glovers Reef, Belize, and on Buoy Reef, Discovery Bay, Jamaica. Although both species have been recorded from Isla Providencia, the collections there were from very different habitats.

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ADDRESSES: (C.R.G.) *Department of Natural Sciences, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-2035;* (J.C.T.) *National Museum of Natural History, Smithsonian Institution (MRC-106), Washington, D.C. 20560.*